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A marine vertebrate fauna from the Late Triassic of Somerset, and a review of British placodonts

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ABSTRACT

The British Rhaetian (latest Triassic) is famous for its bone beds containing abundant remains of fishes and reptiles. Most Rhaetian bone beds are assumed to have been similar in faunal composition, representing long-distance mixing of transported remains, and deposition some distance from shore. In the Mendip Hills of southwest England, some Rhaetian bone beds lie unconformably on Carboniferous Limestone, where the marine sediments of the Rhaetian Transgression lapped onto the shorelines of the palaeo-islands. The fauna from the Marston Road site, near Holwell, Shepton Mallet, in Somerset, shows a remarkable association of some coastal and terrestrial reptile remains mixed with the usual teeth and scales of sharks and bony fishes. We report unequivocal fossils of a small lepidosaur, probably a sphenodontian, a terrestrial wash-in, as well as marine reptiles, the possible thalattosaur *Pachystropheus* and placodonts. Sphenodontian remains are abundant in Late Triassic red bed fissure fills from nearby, and the Marston Road site provides a palaeoecological/ topographic link between terrestrial and marine deposits, hinting also that the development of some of the vertebrate-bearing fissures may have been coeval with the Rhaetian transgression.

Keywords: Triassic, Rhaetian, Westbury Formation, Chondrichthyes, Actinopterygii, Reptilia, Placodontia.

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1. Introduction

The Rhaetian transgression (latest Triassic) extended across much of Europe (Hallam, 1997), including the United Kingdom (e.g. Storrs 1994, Swift and Martill 1999), ending a long period of semi-arid climate with lacustrine and evaporitic sedimentation in a broadly coastal sabhka environment. Occasional storms brought in coarse materials that formed thin horizons of sandstone in the black shales of the Westbury Formation of the Penarth Group (Kent, 1968; MacQuaker, 1987, 1999; Allington-Jones et al., 2010). These horizons include bone beds that contain abundant remains of fossil vertebrates including chondrichthyans, actinopterygians and marine reptiles such as ichthyosaurs and plesiosaurs (e.g. Moore, 1881; Richardson, 1909, 1911; Duffin, 1980, Martill and Swift, 1999; Storrs, 1994).

In the Mendip Hills, the Bristol area and South Wales, folded Palaeozoic rocks represented topographic highs that were not completely submerged by the Rhaetian transgression, but persisted above sea level forming an archipelago of limestone islands (Fig. 3) (Robinson, 1957; Whiteside and Marshall, 2008). Karstic weathering and tectonic activity created fissures in the limestone, which were infilled with sediment. These infills have attracted a great deal of interest since they have yielded remains of early mammals and dinosaurs, such as *Haramiya* and *Thecodontosaurus* respectively (Moore, 1881; Richardson, 1911; Kühne, 1947; Whiteside and Marshall, 2008; van der Berg et al., 2012; Foffa et al., 2014). Dating of the fissures has been problematic, with many being Rhaetian in age, others perhaps older and some younger (Kühne, 1947; Robinson, 1957; Whiteside and Marshall, 2008). In general the faunas of vertebrate-bearing fissures, having formed on the tops of islands, are quite distinct from those of marine, vertebrate-bearing Rhaetian bone beds.

It is uncommon to find a close association between the bedded, marine Rhaetian, especially the Westbury Formation, with its classic phosphatic bone beds, and the terrestrial fissures, of similar age, that formed on the palaeo-islands, and yet one such site is the ‘Marston Road Quarry’, first reported by Charles Moore (1867) in his initial overview of the Rhaetian bone beds and fissures around Bristol, and again by Linsdall Richardson (1909, 1911). The site was mentioned by Kühne (1947, p. 729), in his account of the sedimentology and palaeontology of the nearby Holwell fissure fillings (Fig. 1) and their important early mammal specimens. He reported that Simpson (1928) had dated the Holwell mammals as lower Rhaetian on the basis of the invertebrate fauna recorded by Richardson (1911) from the Marston Road Quarry, ‘about 300 yards east of Moore’s “Microlestes Quarry”, on the other side of the Holwell valley’. Kühne (1947) discounted this dating evidence because it is impossible to be sure that the fissure and the bedded Rhaetian were of the same age.

Nonetheless, the references to the site were intriguing, and we relocated the locality in 2014, on the north side of the A361 road that runs from Frome to Shepton Mallet in Somerset (UK National Grid Reference ST 73114485). Its current state is disappointing, the available outcrop being much reduced in size and almost entirely overgrown. Nonetheless, we located photographs, drawings, and unpublished notes reporting excavations by local geologists Mike Curtis, Charlie Copp and others made during the period 1981–1985. Very little was published of that work, other than a short field description (Copp, 1985), and since then the A361 road has been widened and partly extended over the site of the quarry, so obscuring it for ever. Further, Curtis made substantial collections from the Rhaetian bone bed at this site, comprising 4497 specimens in all, and his collections are available for study, being lodged in Bristol City Museum (BRSMG) and the University of Bristol School of Earth Sciences (BRSUG).

Rhaetian marine vertebrate faunas are generally assumed to have been rather uniform from site to site, presumably reflecting the influence of a single, substantial transgressive event that swept rapidly over the whole of England. Nonetheless, it might be of interest to compare vertebrate faunas from those parts of the Rhaetian that overlie Triassic, and those that accumulated as thinner overlap sequences directly on the margins of the Carboniferous palaeo-islands of the Mendips. Although several studies have investigated the terrestrial fauna from the fissures at Holwell (Kühne, 1947; Copp, 1980; Duffin, 1980), few studies have been undertaken to reconstruct the marine Rhaetian fauna in the Mendip Hills. Whilst stratigraphic differences in invertebrate faunas have been noted in the Westbury Formation (Kent, 1968, 1970), it is generally assumed that the vertebrate fauna shows little or no variation in composition (cf. Sykes, 1971). However, one difference is in the presence or absence of placodonts, marine, shell-crushing reptiles, that have hitherto been described only from Holwell and Aust Cliff (Storrs, 1999); in this paper, we present a new occurrence record from Marston Road. Placodonts were turtle-like, armoured reptiles inhabiting shallow waters in the European epicontinental sea and on the margins of the eastern and western province of the Tethys. They originated in the Early Triassic, probably in Europe (Neenan et al., 2013), diversified through the Mid-Triassic, and became extinct at the end of the Triassic period (Pinna and Mazin, 1993b). They are some of the only reptiles known to have developed a durophagous feeding habit, using their flat, crushing teeth to feed on hard shelled invertebrates such as bivalves and gastropods (Pinna and Mazin, 1993b; Pinna, 1980; Pinna and Nosotti, 1989; Scheyer et al., 2012). The British material consists of isolated teeth and osteoderms, and they are relatively rare (Duffin, 1980). With no articulated specimens, teeth

and osteoderms have previously been assigned to two different genera based on morphology; *Psephoderma* and *Placochelys*. However, Duffin (1980, p. 161) concluded that “it is most unlikely that a toothless *Psephoderma* and an unarmoured *Placochelyan* lived side by side in the British Rhaetian sea”, and the validity of both species has since been questioned (Pinna, 1978; Rieppel and Zanon, 1997; Rieppel, 2000).

In this paper, we describe the Late Triassic geology and marine vertebrate fauna from the Marston Road Quarry. The faunal composition and palaeoenvironment is discussed and compared with other localities in the UK. The record of late Triassic placodonts is also reviewed.

2. Geological setting

The Westbury Formation is the lowest portion of the Penarth Group, which is all Rhaetian (Late Triassic) in age. It is exposed in the south-west of England, Warwickshire, Nottinghamshire and Leicestershire, and consists of pyritic, black shales, with occasional horizons of sandstones and limestones (Kent, 1968; MacQuaker, 1987; MacQuaker, 1999). Towards the centre of the Wessex Basin, the Westbury Formation can be over 10 m thick, but in the Mendip Hills it rarely exceeds 1 m (Duffin, 1980, Kent, 1968). The base of the sequence is unconformable with the underlying Blue Anchor Formation, or in the Mendip Hills with the Carboniferous Limestone. A conglomeratic, basal bone-bed is recorded in many localities, such as famously at Aust Cliff, Avon, and its wide occurrence has attracted a lot of interest in explaining its deposition (e.g. MacQuaker, 1999; Suan et al, 2012). However, in the Mendip Hills and elsewhere, bone-beds are found throughout the sequence (Kent, 1968; MacQuaker, 1987; Storrs, 1994). The bone beds are rich in vertebrate remains, but the most common Rhaetian fossils are bivalves, usually found in shell beds (Macquaker, 1987). Bone-beds and shell beds often cap coarsening-upwards units within the formation, indicating sedimentary cyclicity - the pyrite in the black shales suggests anoxic seafloor conditions, whereas the fossiliferous sand and limestone horizons have been interpreted as storm deposits (MacQuaker, 1987; Wang, 1993; Allington-Jones et al., 2012).

The Holwell area was pivotal in studies of the British Mesozoic. Charles Moore (1815–1881) began to explore the geology south of Bristol and Bath in the 1850s, focusing initially on the area around Holwell because there was a spectacular unconformity between the Carboniferous Limestone and Inferior Oolite at Vallis Vale. There he collected marine fossils from the Inferior Oolite, but also for the first time located fissures in the Holwell Quarries, cutting the Carboniferous Limestones, and filled with Mesozoic sediments and

fossils, probably making his discovery in 1855 or 1856 (Savage, 1993). Moore reported these at the British Association meeting in 1858 (Moore, 1859), led a field trip in 1864, and later outlined his conclusions in detail (Moore, 1867), providing the first evidence for the occurrence of rocks equivalent to Gmbel's (1861, p.356) "Rhaetische Gruppe" in the United Kingdom. His conclusion was based on a combination of field stratigraphy, identifying the Inferior Oolite (Middle Jurassic), the underlying Lias (Lower Jurassic), and the bedded, bone-bearing Rhaetian below. Importantly, this field evidence was backed by palaeontological data: Moore (1867) collected large volumes of fossiliferous sediment, and extracted thousands of microvertebrate remains from the fissures in the Holwell quarries and from the bedded Rhaetian at Marston Road. In the southern Holwell quarry, he identified teeth of the mammal 'Microlestes', later renamed *Haramiya*, comparing it with near-identical specimens previously identified by Plieninger (1847) from the Rhaetian bone bed at Degerloch, in Wrttemberg, south-west Germany. Associated with the German 'Microlestes' were teeth and scales of classic Rhaetian taxa such as *Acrodus* (now *Lissodus minimus*) and *Gyrolepis*. Warrington (1984) reported a sample from Marston Road with palynomorphs indicative of Rhaetian age.

The Marston Road site was hard to locate, and had almost been lost. Moore (1867, pp. 482–483) noted the location 'Just above the hamlet of Holwell, in the direction of Marston, a small roadside section of about 10 feet in depth by about 30 yards in length... At this spot large quarries of Carboniferous Limestone in the valley below are to be observed'. He described the occurrence of Carboniferous Limestone at the base, superseded by Rhaetian, Lias, and Inferior Oolite. He stated that 'The Rhaetian deposits are represented in the western end of this section by a friable marl, about 10 inches thick, in which occur teeth of *Acrodus*, *Sargodon*, &c., and vertebrae of *Lepidotus*, whilst in the floor of the quarry the Carboniferous Limestone is seen. To add to this remarkable variety, a mineral vein, 8 feet in thickness, has been left standing towards the roadway, and has met the base of the Inferior Oolite; and there are also two caverns in the Liassic limestone which have not been explored.' Moore (1881, p. 68) referred again to the Rhaetian sections at Holwell and Nunney, but gave no further specific information about the Marston Road section. He did, however, make a large sketch painting of the section, probably used for educational purposes, which is now housed in the Bath Geology Museum (Fig. 4). Also kept in the Bath Geology Museum is a photograph of the section, presumably taken by Moore on one of his field trips to the site (Fig. 5). The photograph is annotated, showing the succession of Inferior Oolite, Rhaetian sediments and

Carboniferous Limestone. Neither of these images is dated, but we assume they were taken some time in the 1850s or 1860s.

The quarry was visited twice by field trips comprising members of the Geologists' Association, first in 1890, and then in 1909. On the 1890 trip, Winwood and Woodward (1890, p. clxxiii) reported the Marston Road section as 'some 10 ft. in depth and 90 ft. in width', and exposing Inferior Oolite at the top, lying unconformably on Carboniferous Limestone. No mention was made of the Lias or Rhaetian. Later, during the 1909 trip, Richardson (1911, p. 220) reported that 'At the Marston-Road Section the Rhaetian breccia containing fish-remains was soon discovered firmly fixed on to the here irregular Carboniferous-Limestone surface, and many more examples of the characteristic Rhaetian fish-remains were procured from the succeeding layer of yellow shaly matter. Another thin bed of Rhaetian impure limestone follows, and then comes the Lias – mainly a whitish sparry rock with its top-portion conspicuously bored by *Lithophagi*. On this bored surface rests the Inferior Oolite containing *Acanthothyris spinosa* (Schlotheim), etc.' The party then headed west to a rock face behind the Bear Inn and Paddington Cottage, where they explored a vertical fissure fill in the Carboniferous Limestone (located at ST 72834502). Both sites may still be seen, separated by 330 m, within which distance the Carboniferous Limestone emerges to an exposed height of some 5 m owing a dip in the land.

Based on this visit, and an earlier one in 1908, Richardson (1911, p. 62) presented further details, noting the succession as:

Inferior Oolite	Limestone, hard, dense, conglomeratic at the base	2 ft 0 in (61 cm)
Lias	Limestone, hard, whitish, sparry, pebbles of pure white limestone (?Langport Beds) at the base. Top portion, considerably bored by <i>Lithophagi</i>	Variable in thickness
Rhaetian (Westbury Beds)	Limestone, somewhat sandy and earthy, with fragments of Carboniferous Limestone	0 ft 4 in (10 cm)
	Shale, yellow, gritty, calcareous	0 ft 6 in (15 cm)
	Breccia in intermittent patches, firmly adherent to the Carboniferous Limestone	0 ft 2 in (5 cm)
Carboniferous	Carboniferous Limestone, presenting a very irregular surface	

In the three divisions of the Rhaetian, he noted fossils in each: *Acrodus minimus*, *Gyrolepis alberti*, and vertebrae in the upper sandy limestone, fragments of *Pteria contorta*, *Chlamys valoniensis*, and *Protocardia* in the middle shale, and 'usual fish-remains' in the lower

Rhaetian breccia, namely the basal bone bed. Richardson (1911, pp. 62-63) goes on to describe the wall of Carboniferous Limestone with a fissure behind the Inn, and then, across the Frome-Shepton Mallet road, on its south side, the '*Microlestes* Quarry' of Moore (1867), at ST 725449. This is Cree's Quarry, according to Wall and Jenkyns (2004, fig. 8), as distinct from Coleman's Quarry on the north side of the A361, centred on ST 727454. Cree's Quarry, confusingly, is called 'Coleman's Quarry' on the Ordnance Survey map. Further north of Coleman's Quarry proper, where Moore (1867) first observed numerous subvertical fissures, are North Quarry and Bartlett's Quarry (Wall and Jenkyns, 2004, fig. 8). All these quarries lie on the west side of the Holwell Valley and Nunney Brook.

The Marston Road site was rediscovered and cleared by the Nature Conservancy Council in 1981 as a conservation and research exercise (Copp, 1985). Charlie Copp, Mike Curtis, and members of Bristol-based amateur geological societies worked hard to remove vegetation, and extensive collections were made, and field notes carefully taken. In the only published account, Copp (1985) noted that the 'new section is difficult to relate to the previously published descriptions, and has proved to be considerably more complex than hitherto realised. The back of the quarry consists of a low platform of Carboniferous Limestone, faulted against Rhaetian clays, sands and gravels which are overlain unconformably by Inferior Oolite. The Rhaetian sediments are rich in fish remains and some large reptile bones have been found in the gravels including a tooth of '*Thecodontosaurus*.'

The Marston Road site was also known for a cave at ST 73114484, called Tom Tivey's Other Hole, extending some 4 m deep into the Carboniferous Limestone, but this was covered and partially destroyed, as was the remainder of the Marston Road Quarry, by the building of the Nunney Catch bypass on the A361 road in 1985–1987 (Vranch, 1988). The remaining portion of the quarry is only the northernmost part, now substantially overgrown and with only the uppermost exposure of Inferior Oolite still visible.

The Westbury Formation is described as lying unconformably on Carboniferous limestone, followed by the Cotham beds, Langport beds and the Jurassic Inferior Oolite (Moore, 1867; Richardson, 1911). The Cotham and Langport beds consist of micritic limestones, believed to have formed during a temporary regression in the late Rhaetian, before a second transgression turned the area fully marine in the Hettangian (Swift, 1995; Hallam, 1997; Hesselbo et al., 2004). Curtis measured the Rhaetian sediments to be 0.5 m thick, consisting of yellow limestone shales, sandstone beds and black clays (Fig. 6). The great majority of our samples were taken from a bone bed close to the base of the Westbury Formation, described by Curtis as "buff, sandy conglomerate". One sample was taken from a

gravelly sandy layer towards the top of the section. No obvious basal bone bed is described in Curtis' notes, although older publications mention Rhaetian vertebrate remains in either friable marl (Moore, 1867, p. 482) or a conglomeratic basal layer (Richardson, 1911, p. 62). There are other marked differences between Moore's (1867) and Richardson's (1911) descriptions of the site, and the more recent ones by Copp (1985) and Curtis. The sides of the quarry were described as being faulted by Copp (1985), and instead of the continuous sequence of the Westbury Formation, Cotham beds, Langport beds and the Inferior Oolite, Copp reported that the Inferior Oolite lay unconformably on the Rhaetian beds, and that the Langport beds were 'folded down' over the Carboniferous limestone at both ends of the quarry. Copp (1985) also described fissures in the eastern and western parts of the section. These unconformities and fissures are visible in Curtis's photographs of the quarry (Fig. 7). The reason neither Moore nor Richardson mention this more complicated geology of the Marston Road section is probably because they did not have such an extensive view of the cleaned outcrops, and the site was changed by the 1981 excavation and the 1985-1987 roadworks (Copp, 1985; Vranich, 1988), and these features were not visible earlier. This is obvious when comparing Moore's photograph and sketch of the quarry (Figs. 4-5), with Curtis's photographs (Fig. 6-7).

Based on their exploration of the Marston Road quarry at its best exposed, Copp (1985) reconstructed a sequence of seven events in the accumulation of the Triassic and Jurassic strata:

1. Deposition of the Rhaetian sands, clays and gravels on the Carboniferous Limestone surface.
2. Deposition of later Rhaetian sediments (Cotham and Langport Formation limestones).
3. Deposition of Lower Jurassic (Lias) limestones.
4. Step-faulting and fissure formation along east-west lines. Carboniferous Limestone downfaulted with respect to the Rhaetian sediments at the back of the quarry. Lower Jurassic and some Rhaetian limestones collapsed into a fissure at the front of the quarry. Rhaetian limestones downfolded as pressure opened the fissures.
5. Period of denudation, followed by deposition of lower units of the Inferior Oolite.
6. Further fault movement at the back of the quarry; Rhaetian sediments downfaulted with respect to the Carboniferous Limestone.
7. Further denudation, followed by deposition of upper units of the Inferior Oolite.

3. Materials and methods

The fossil material used in this study was collected by Mike Curtis during 1982-1985 from the Westbury Formation of the Marston Road Quarry (ST 730449), Somerset. His collection was donated to the University of Bristol and the Bristol Museum and Art Gallery after his death in 2009. Most of the samples were already processed and sorted by Curtis, who describes his method in his notes. The samples were washed, dried, and then sieved through 4 mm, 1.2 mm and 500 μ m sieves. The material smaller than 500 μ m was then covered in water, and silt was removed by decanting the fluid. This sample was dried and treated with 10% acetic acid, and silt was again removed by decanting. Finally, the sample was dried. The fossil material was picked out from all washed samples, and sorted according to species, or if not possible to identify, placed in different groups; scales, denticles, bone fragments, and unidentified teeth. These methods are described further by Korneisel et al. (2015).

Curtis's material has been checked and identified by us, and the number of specimens counted. In order to estimate relative abundances of each species, we distinguished identifiable and unidentifiable material, counting shark teeth with the major cusp present, and actinopterygian teeth with at least 70% of the crown intact, and these were distinguished from fragments of teeth (cusplets, crown fragments and isolated roots). For scales and denticles, no distinction was made between fragments and whole specimens.

In addition, one placodont tooth was provided by C.J.D., collected from Marston Road Quarry in the 1980s.

4. Systematic palaeontology

4.1. *Chondrichthyans*

Six species of shark have been identified from the Marston Road Quarry, all known previously from the Westbury Formation (Duffin, 1999).

4.1.1. *Lissodus minimus* (Agassiz, 1839)

The teeth are low crowned, and diamond-shaped in occlusal view, often with the mesial and distal ends slightly curved to the lingual side, creating a concave shape in occlusal view (Fig. 8A-D). They range in size from 2-7 mm mesiodistally. The central cusp ranges from medium height in anterior teeth, to low in lateral and posterior teeth. Two or four pairs of lateral cusplets may be present, which are very low in height. A longitudinal ridge (the occlusal crest) extends from end to end of the tooth, dividing the cusp, and in most specimens vertical ridges extend downwards from this crest and from the apex of the cusp, on both labial and lingual sides of the crown. The ridges are generally non-branching, but may bifurcate at

the lower half of the crown. A labial peg is present, protruding from the lower half of the labial side of the cusp, but becomes significantly less pronounced laterally through the dentition. The crown base is concave. The root is rarely preserved, but when intact has large vascular foramina and a flat or slightly concave base. At the upper portion of the root on the labial side, a ridge with smaller, vascular foramina runs parallel to the crown base.

As with many other selachians, the teeth vary in morphology depending on their position in the jaws. Two main morphologies could be determined, representing anterior and lateral teeth (Duffin, 1985), with many intermediate forms.

Anterior teeth: These teeth have long and narrow crowns, and a high, sharp cusp (Fig. 8A-B). They often have two or four lateral cusplets, which are very low in height. The mesial and distal ends of the cusp are slightly curved to the lingual side, creating a concave shape in occlusal view. The labial peg is well developed. Anterior teeth have fewer vertical ridges, sometimes only one major vertical ridge on the labial side, extending up the crest of the labial peg and ascending towards the apex of the central cusp.

Lateral teeth: Lateral teeth are more robust, having a lower crown profile and being much wider labiolingually (Fig. 8C-D). They are dome-shaped and the central cusp barely rises above this baseline. Lateral cusplets are absent or very low. The teeth have a clear diamond shape in occlusal view, and the ends are not curved towards the lingual face. The labial peg is absent or very small. An occlusal crest extends along the long axis of the tooth, but is less pronounced than in anterior teeth. The crown faces are ornamented by several vertical ridges.

4.1.2. *Hybodus cloacinus* (Quenstedt, 1858)

These teeth are similar to *R. minor* (see below), but are more elongate, have a lower crown, a less sharp apex of the major cusp, and often three or more pairs of cusplets laterally (Fig. 8E-F). The central cusp and lateral cusplets are lingually inclined and the crown has vertical ridges descending from the apices of the central cusp and lateral cusplets, and from the occlusal crest. The base of the crown is concave, and the crown-root junction is incised on both labial and lingual sides, although the feature is more pronounced lingually. The root is bulbous and lingually offset, and has numerous vascular foramina. The root base is concave.

4.1.3. *Synechodus Rhaetianus* (Duffin 1982)

S. Rhaetianus teeth are elongate with a high crowned, symmetrical central cusp (Fig. 8G-I). It is flanked by one or up to four pairs of lateral cusplets in posterior teeth. The first

pair of lateral cusplets are half the size of the central cusp, and the following pairs decrease in size at the same rate mesially and distally. The central cusp and lateral cusplets are lingually inclined. The crown is ornamented by vertical ridges that descend from the apices of the central cusp and lateral cusplets, and from the occlusal crest. At the base of the crown, these ridges form a reticulate pattern, covering approximately one third of the cusp height on the labial side and one sixth of the crown height on the lingual side. The base of the crown is concave, and the root-crown junction is incised on both labial and lingual sides. The root, which is usually present, protrudes lingually, and is scalloped with a concave lower portion on the labial side. It has large vascular foramina, and the base is slightly concave.

S. Rhaetianus shows monognathic heterodonty (Duffin, 1998a), and both anterior (Fig. 8G-H) and posterior (Fig. 8I) teeth are present in the sample, as well as several intermediates. Posteriorly through the dentition, the crown decreases in height from high to very low, and the number of lateral cusplets increases. The reticulate pattern at the base becomes less pronounced, and the root becomes shallower.

4.1.4. *Rhomphaiodon minor* (Agassiz, 1837)

The teeth are high crowned and with a symmetrical central cusp (Fig. 8J-K). The cusp is sharply pointed and flanked by one or two pairs of lateral cusplets, measuring about a quarter of the height of the central cusp. Both the central cusp and the lateral cusplets are lingually inclined. The crown has a well-developed occlusal crest that forms cutting edges to the central cusp and lateral cusplets, and vertical ridges descend from the apices of the central cusp and lateral cusplets, sometimes bifurcating at the base of the crown. The base of the crown is concave, and the crown-root junction is not incised. The root is bulbous and lingually offset, bears large vascular foramina, and has a flat or slightly arched base.

4.1.5. *Pseudodalatias barnstonensis* (Sykes, 1971)

One fragmentary tooth was identified as *P. barnstonensis* (Fig. 8Q). The tip, root and part of the side is missing, but the angle of the edges of the crown indicates a triangular and symmetrical shape in lingual view. The cutting edge of the tooth is strongly serrated, with four serrations per mm. Labio-lingually, the tooth is flattened but slightly concave on the lingual face, forming a longitudinal depression in the central part of the crown. *P. barnstonensis* shows strong dignathic heterodonty - upper teeth lack serrations and are not flattened but circular in cross section, and have an elongate, pointed and lingually curved central cusp (Duffin, 1980). Teeth also vary laterally through the dentition, with lower teeth

showing increasing asymmetry distally. The symmetrical crown of our specimen, and comparison with figures in Sykes (1971) indicates it is a lower symphyseal tooth.

4.1.6 *Duffinselache holwellensis* (Duffin, 1998)

This taxon is represented in the sample by elongate teeth with a low crown, usually lacking lateral cusplets, although larger specimens sometimes have weakly developed lateral cusplets (Fig. 8L-M). The central cusp is low and asymmetrical, inclined distally at an angle of 45°. It is slightly offset from the mid-point of the crown, and has two prominent ridges descending from the apex of the central cusp, bisecting it labio-lingually. Smaller vertical ridges ornament the lower crown on the sides of the central cusp, extending basally from the occlusal crest. These are straight and non-branching. Sometimes, additional fine ridges can be seen on the central cusp as well. The mesial part of the tooth is slightly bent lingually in occlusal view. The base of the crown is flat. The root, which is usually present, constitutes two thirds of the crown height. It has numerous vascular foramina and is weakly inclined lingually. The base of the root is flat. Some variation is seen in this sample of *D. holwellensis* - smaller teeth have a lower cusp which is less inclined, and larger specimens sometimes show weakly developed lateral cusplets. This has been interpreted as representing weak monognathic heterodonty (Duffin, 1998b).

4.1.7. *Pseudocetorhinus pickfordi* (Duffin, 1998)

A single tooth is assigned to this species. The cusp is asymmetrical, with its axis inclined at 45° to the vertical, as well as being lingually inclined (Fig. 8O-P). The enameloid surface is smooth and lacks ornamentation, and the mesial and distal extremities of the crown are rounded. Lateral cusplets are absent. The robust root protrudes lingually, where it constitutes a third of total tooth height. On the labial side, the root is shallower, about a tenth of tooth height. It has vascular foramina and the base is slightly concave. The tooth measures 4 mm mesio-distally, and 2 mm in height.

4.1.8 *Other selachian remains*

Denticles: Over 200 denticles were found in our sample. Isolated denticles are hard to assign to a particular taxon, since they vary greatly in morphology depending on the age of the shark, and their location on the body (Duffin, 1999). However, they can be sorted into groups based on their morphology. Three types of denticles were common in our sample:

placoid, hybodontoid and ctenacanthid scales (following Reif, 1978). More rare are the chimaeriform scales, described by Sykes (1974).

Placoid scales: These denticles can be divided into two groups, type 1 and type 2, which have slightly different morphologies. Type 1 has a concave, elliptic base from which a posteriorly inclined crown with a sharp tip extends. The crown is slender and has vertical ridges on the dorsal side, descending from the tip of the crown to the basal plate. Type 2 has a flat, circular base, with a leaf shaped, recurved crown that gives it a quadrate outline in dorsal view. The crown bears vertical ridges dorsally. Type 1 and 2 scales constitute the two ends of a continuum of intermediate forms. Type 3 is distinct from 1 and 2 by having a very low crown with a smooth, flat top. The crown extends from a cylindrical pedicel with coarse vertical ridges and foramina. Similar scales have been described from the Lower Lias of Lyme Regis, found in the oral cavity of *Palidiplospinax* (Duffin and Ward, 1993).

Ctenacanthid scales: The second type of chondrichthyan denticle has a rectangular, flat base with several, recurved, elongate crowns. The crowns are laterally fused and have pronounced ridges extending from the apices towards the basal plate, giving the enamel a “wrinkled” appearance.

Chimaeriform: These denticles have a bulbous basal plate, oval in shape, with numerous foramina. Each one is cone-shaped with an inclined, low, smooth enameloid cap covering the top surface. The denticles vary slightly in shape and size, with some being flatter ventral-dorsally. These resemble holocephalan denticles figured by Korneisel et al. (2015, fig. 6).

Prismatic cartilage: Ten pieces of prismatic cartilage are present in the collection. Individual tesserae are hexagonal, 1mm wide and 0.5mm thick. Prismatic cartilage is composed of apatite and covers parts of the cartilaginous skeleton of chondrichthyan fishes, providing extra strength (Dean and Summers, 2006). It is believed to be a chondrichthyan synapomorphy (Maisey, 1986), found in all extant forms and known from early fossil forms (Miller et al., 2003).

Neoselachian vertebrae: Thirteen vertebrae are present in the collection, each being cylindrical with a concave centrum. Three partial vertebra were also recorded, where only part of the centrum has been preserved. These are dome-shaped with concentric rings. The largest vertebra measures 10 mm in diameter and 4 mm in thickness, and the smallest 2 mm in diameter and 2 mm in thickness. The vertebrae are of cyclospondylous type.

4.2 Actinopterygians

Six taxa of bony fish were identified from the collection, all previously known from the British Rhaetian.

4.2.1. *Gyrolepis albertii* (Agassiz, 1835)

The teeth are cone-shaped and the root is curved to one side (Fig. 9A). The apical enamel cap has a smooth surface, and constitutes 25% or less of the total tooth height. The root increases in diameter as it extends downwards from the cap, and may possess vertical striations. The teeth in the collection vary in size from 2-3 mm high, and also show varying degrees of ante-mortem wear.

4.2.2. *Severnichthys acuminatus* (Agassiz, 1844)

Birgeria acuminata-type: These teeth are abundant in the collection. They are cone-shaped, and sometimes recurved (Fig. 9F). The crown constitutes half or more of the total tooth height, and is separated from the root by a circumferential ridge. The tip of the crown, or in smaller teeth the entire crown, is sometimes translucent. Relatively coarse vertical ridges descend from the tip of the crown, and the root has fine, vertical striations.

Saurichthys longidens Agassiz, 1835-*type*: Six teeth in the sample belong to the *Saurichthys longidens*-type; they are conical with a smooth cap, which constitutes less than half of the tooth height (Fig. 9B-E). Below the cap the crown has pronounced vertical ridges. The root is not preserved in any of our specimens. The teeth show considerable variation in both size and morphology - some are slightly curved, tending towards sigmoidal in lateral view (Fig. 9B-C). A distinct junction, sometimes ridged may occur between the cap and the rest of the tooth (Fig. 9B-D), and the ridges below the cap may be fine (Fig. 9C) or more coarse (Fig. 9D).

Remarks. Isolated teeth of *Saurichthys longidens*-type and *Birgeria acuminata*-type were originally classified as two separate species, on basis of their different tooth morphologies (Stensiö, 1925). However, fish teeth can vary greatly depending on their location in the mouth, and Storrs (1994) described a jaw that contained both types of teeth. He synonymised the two species, and allocated them to the new genus *Severnichthys*.

4.2.3. *Sargodon tomicus* (Plieninger, 1847)

Two types of teeth have been assigned to this species, described by Duffin (1980) as incisiform and molariform.

Incisiform: The tooth is flattened and the occlusal surface of the crown has a u-shaped profile in lingual view, produced by ante-mortem wear during feeding (Fig 9G). The crown is taller medially. In occlusal view, the tooth has a slightly triangular outline, being wider medially and tapering out laterally towards the tip. The root is long, constituting around four fifths of the tooth height, and is not separated by a ridge from the crown. The crown has no ornamentation, but the root has fine, vertical striations. The worn occlusal surface reveals the distinctive arrangement of vascular canals penetrating the dentine and overlying acrodin cap from beneath, giving the surface of the crown a somewhat spotty appearance.

Molariform: The majority of the teeth in the collection belong to this morphotype. They are dome-shaped and circular or elliptical in occlusal view (Fig. 9H). The root is short, about the same height as the crown, and has fine striations. The occlusal surface of the tooth often shows signs of ante-mortem wear, being flattened or sometimes with a rise slightly offset from the centre of the tooth. Vascular canals are sometimes visible on the occlusal surface. The teeth are frequently preserved without the root, and vary in size from 2 mm to less than 1 mm in diameter.

4.2.4. “*Lepidotes*” *sp.*

Lepidotes teeth are of two types. The first type is very similar to molariform teeth of *S. tomicus* – dome-shaped, elliptical in occlusal view, and having a short root (often absent) with striations. In the second type, the root is usually present and constitutes two thirds or more of the total height (Fig 9I). The root is bulbous and sometimes shows fine striations. A rounded peg protrudes from the root, which in small teeth is translucent, but blackened in larger teeth. This type is usually smaller in size than the molariform teeth.

Lepidotes is, similarly to *Colobodus*, a name that has been applied to various, dome-shaped durophagous teeth from Triassic and Jurassic strata (López-Arbarello, 2012). Isolated teeth lack distinguishing characters, which makes it difficult to differentiate them from other semionotid taxa like *Paralepidotus*. In the absence of more articulated specimens, and since this type of teeth from the British Rhaetian has historically been described as *Lepidotes* *sp.* (e.g. Duffin, 1980, Moore, 1867, Richardson, 1911, Sykes, 1979), we retain the name here for continuity.

4.2.5. *Semionotid cf. Colobodus sp.*

These teeth are dome-shaped with a short, acrodin cusp on the occlusal surface (Fig. 9J). The cusp is translucent and sometimes heavily worn. The enamel below the cusp has

pronounced, vertical, straight and non-bifurcating ridges running down the cusp, and is often shiny black. The shape of the crown varies, with marginal teeth being taller and a second type of tooth being more flattened. The root is not present in any of the teeth in the collection, and the crown is often broken at the base.

Colobodus sp. is a problematic taxon with a complicated history. Originally described by Agassiz in 1844 (Agassiz 1833-1844), who failed to illustrate the specimen, the name has since been applied to various crushing-type teeth found in the Triassic. In a review of the family Colobodontidae, Mutter (2004) established the genus *Colobodus* on the basis of the type species, *C. bassanii*, described by Alessandri (1910). However, he considered the range of this genus to be Anisian-Ladinian, regarding the identification of Late Triassic teeth as *Colobodus* sp. “ambiguous if not erroneous” (Mutter 2004, p. 204). The teeth can easily be confused with those of other semionotid fishes with a similar lifestyle, such as *Paralepidotus* (Mutter, pers. comm.). Even so, the teeth described above are distinct with a central acrodin cap, longitudinal ridges and a conical to dome-shaped appearance. Similar teeth have previously been described as *Colobodus* from Rhaetian faunas in Luxembourg (Delsate and Duffin, 1999), and in Britain from Holwell, Aust Cliff and Leicester (Duffin, 1980, Horwood, 1916). Acrodin caps are found in juvenile *Paralepidotus* teeth, but lack vertical striations (Bürgin and Furrer, 2004, Lombardo and Tintori, 2005, Lopez-Arbarello, pers. comm., Tintori, 1996, Tintori, 1998). However, the lack of articulated specimens makes it difficult to assign these teeth to any particular species with certainty.

4.2.6. Other actinopterygian remains

Scales: Fish scales are the most common fossils in the collection. They are rhombohedral and measure 5-10 mm diagonally. Some are very worn, and in these scales the enamel of the outer surface is no longer present and only concentric rings can be seen. When the enamel is preserved, it is shiny black and either smooth or with branching ridges. Scales are very difficult to assign to species, especially since they vary in shape depending on their location on the body of the fish, but *Colobodus* and *Gyrolepsi albertii* scales have been described from the British Rhaetian (Sykes, 1970). The great majority of our scales, which have branching ridges would, according to these descriptions, be from *Gyrolepis albertii*.

Fin ray elements: Numerous fin rays elements are also present, which are cylindrical and laterally flattened, giving them an elliptical cross section. The base, which is usually preserved, is flat or angled, and as the spine extends it tapers. Fine striations along the length

of the fin ray are usually present. All of our specimens are broken off at the distal end. They range in size from 1-2 mm long.

Vertebral hemicentra: Thirteen hemicentra from actinopterygian vertebra are identified. These are thin and arched in posterior-anterior aspect.

Jaw fragments: Eleven jaw fragments are present in the collection, of which some are very fragmentary. BRSUG 29371-1-92/4 (Fig. 9P) is an elongate jaw fragment which is flattened dorsally and convex ventrally. The teeth are dome-shaped and circular in occlusal view, and bear an acrodin cusp. They resemble the teeth of “*Lepidotes*” sp. The jaw measures 2 mm mesio-distally, but is broken at the ?distal end. The teeth are 0.25 mm tall. BRSUG 29371-1-92/1 is broken at both ends and holds three whole and one fragmentary tooth of *Colobodus* sp. type (Fig. 9K-L). The translucent cusp is completely worn down on all teeth. The jaw has a flat base and is 2 mm in length, with teeth measuring 0.5 mm in height. A third jaw fragment, BRSUG 29371-1-92/3 (Fig. 9O) has very similar teeth, but these are smaller, and the enamel is light brown instead of the normal black. In all other aspects they resemble *Colobodus* teeth; the teeth are dome shaped and have vertical ridges descending from the tip of the crown, and the tip is slightly lighter in colour, suggesting a worn down peg. The jaw measures 2 mm in length and holds six teeth.

Most jaw fragments look similar to BRSUG 29371-1-92/2 (Fig. 9M-N), with smooth, dome-shaped and very worn teeth of different size and numbers. These tooth plates are typical for durophagous fish, but abrasion and the often very fragmentary state of the plates makes it hard to differentiate between different taxa. It is currently unclear as to which of the tooth-bearing elements in the jaw complex these specimens might belong.

4.3. Reptiles

4.3.1. *Pachystropheus raeticus* (Huene, 1935)

Four incomplete vertebrae are assigned to *Pachystropheus raeticus*. Three of the specimens are fragmentary centra (BRSUG 29371-1-826:1 and 2, Cc5890). These are compressed laterally in the medial portion, with a flared end and oval, flat articular faces (Fig. 10G-H).

BRSUG 29371-1-826:3 (Fig. 10A-B, E-F) is the most complete vertebra, but it is abraded and missing transverse and articular processes. The centrum is elongate, approximately twice as long as it is tall, and laterally flattened. Articular faces are oval and convex - however, the convex shape may be a consequence of abrasion, since *P. raeticus*

vertebrae are generally amphicoelous (Storrs, 1994; pers. obs.). The neural foramen is triangular in outline, and the neural spine thin and sub rectangular in lateral view.

Remarks. In earlier literature, *P. raeticus* is mentioned as *Rysosteus oweni*. This genus was originally created by Owen (1842), in describing a vertebra from Aust Cliff. However, his description of the specimen (now, seemingly, lost) was insufficient to characterise the genus, and Huene (1933) later assigned similar material from Blue Anchor Point to *Pachystropheus raeticus*, a species also known from strata of similar age in Germany. This rendered *Rysosteus oweni* a nomen dubium.

4.3.2. *Psephoderma alpinum* (Meyer, 1858)

One complete tooth, and a small fragment of a tooth are identified as belonging to the placodont, *Psephoderma alpinum*. The tooth is dome-shaped, slightly oval in occlusal view and the enamel is smooth and shiny black (Fig. 10C-D). In occlusal view it measures 42 mm along the long axis, 33 mm along the short axis, and the thickness is 13 mm. The occlusal surface bears an arcuate groove adjacent to one margin of the crown which, on comparison with figures of a complete skull in Pinna (1976), suggests that the Martson Road specimen is a posterior maxillary tooth. Because of their superficial similarity, *Psephoderma alpinum* teeth may have sometimes been mistaken for larger specimens of *Lepidotes*.

The placodont remains from the British Rhaetian were originally assigned to two different genera, *Placochelys* and *Psephoderma* (Duffin, 1980). Osteoderms described from the Holwell fissure filling material were assigned to *Psephoderma anglicum* (Meyer, 1867), and teeth to *Placochelys stoppanii* (Osswald, 1930). However the differences in morphology between these new species were found to be within the frame of ontogenetic variation of *Psephoderma alpinum* (Pinna, 1978). *Psephoderma anglicum* and *Placochelys stoppanii* were subsequently synonymised with *Psephoderma alpinum* (Pinna, 1978; Rieppel and Zanon, 1997; Rieppel, 2000). In the light of these developments in placodont classification, and the fact that no osteoderms have ever been found from *Placochelys stoppanii* and no teeth from *Psephoderma anglicum*, the most parsimonious explanation is that the British placodont material should all be assigned to the single species *Psephoderma alpinum*.

4.3.3. *Lepidosaurus*

Four bone fragments (BRSUG 29371-1-882/1-4) were identified as being lepidosaur, and probably sphenodontian origin. All have a polished, abraded appearance from post-mortem transport.

BRSUG 29371-1-882/1 (Fig. 10I-J) is identified as a metatarsal or phalanx (Whiteside pers. com.), and has a slender shaft with a laterally expanded head. The head is slightly more expanded on one side than the other. The bone is flattened dorso-ventrally, and one end is broken and abraded. It measures 1.3 mm in length, and the width is 1 mm at the head and 0.5 mm across the shaft.

BRSUG 29371-1-882/2 (Fig. 10K-L) is a metatarsal (Whiteside pers. com.), broken at the proximal end. The bone is flattened dorsoventrally, giving the shaft an elliptical cross section, and the head is slightly expanded. The dorsal side has a central groove running along the posterior-anterior axis. The ventral side bears a longitudinal ridge, and the head is slightly convex in lateral view. It measures 1.2 mm in length, and the widths of the head and shaft are 0.6 and 0.4 mm respectively.

BRSUG 29371-1-882/3 (Fig. 10M) is an 1.5 mm long and 0.7 mm wide bone fragment, broken at both ends. It has no curvature, but is straight and with a circular cross section.

BRSUG 29371-1-882/4 (Fig. 10N) measures 3.5 mm in length and 1 mm in width at its widest end. It is triangular in cross section, with two concave sides. One end is expanded and flattened. The bone is broken at both ends.

4.4. *Other fossilised remains*

4.4.1. *Coprolites*

Coprolites are common in the Westbury Formation, presumably produced by the fishes and marine reptiles (Duffin, 1979). In this study, 14 coprolites were found, ranging from 1-2 mm in length. They vary in shape, being sub-spherical, conical, triangular and flattened, or elliptical and flattened, as well as in colour, ranging from shiny black to dark brown, light brown and grey. Several, lighter coloured coprolites contain scales.

4.4.2. *Bone fragments*

Almost 500 bone fragments could not be assigned to taxa. These have a great variety of shapes, and range in size from 1-5 mm. They also vary in abrasion state, where some fragments are subrounded and others subangular or angular.

5. Discussion

5.1. Faunal composition

In terms of species lists, the chondrichthyan and actinopterygian fauna of the Marston Road collection is very similar to fossil assemblages from other parts of the Westbury Formation, as recorded from localities in the Mendip Hills (Moore, 1867; Richardson, 1909, 1911; Copp, 1980; Duffin, 1980; Swift, 1999) and outcrops in Nottingham and Leicester (Horwood, 1916; Sykes, 1970; Duffin, 1999). When all 4497 specimens are considered, including fragmentary teeth, a third (33%) consist of scales (Fig. 11A). Chondrichthyan and osteichthyan teeth contribute 25% and 15% respectively, and unidentifiable bone fragments account for 18% of the collection. The slightly higher value for chondrichthyan teeth compared to osteichthyan teeth may be because the former are more prone to breaking. This becomes clear when tooth fragments are subtracted from the counts, resulting in a lower number of chondrichthyan teeth compared to osteichthyan teeth (48% and 52% respectively). In this count of teeth, three species dominate: *Lissodus minimus*, *Gyrolepis albertii* and *Severnichthys acuminatus* (Fig. 11B). Together, they constitute 80% of the teeth in the samples. Few quantitative studies of fossils from the Rhaetian bone beds have been completed, but a comparison with the recent study of basal Rhaetian bone bed material from Blue Anchor Point by Korneisel et al. (2015) shows an overall similarity in distribution and diversity. The differences in percentage are probably a consequence of differences in counting criteria and sample sizes, rather than a significant variation in fauna.

Ichthyosaur and plesiosaur remains are occasionally found in the Westbury Formation, yet none was found in our sample from Marston Road. Curtis lists ichthyosaur remains in his notes, but these specimens seem to have been lost. However, four vertebrae from the semi-aquatic reptile *Pachystropheus raeticus* are present, one nearly complete and three fragmentary. *P. raeticus* has previously been described in the Westbury Formation from Holwell (Kühne, 1947), Aust cliff, Garden cliff, and Westbury on Severn (Owen, 1842; Browne, 1894). One placodont tooth is also described, identified as the cyamodontid *Psephoderma alpinum*. Placodont teeth are rare in the Westbury Formation, having only been found previously at Aust Cliff and Holwell (Kühne, 1947; Duffin, 1980). Copp (1985) mentioned a thecodontosaur tooth from the Marston Road quarry, but unfortunately there is no reference to when the tooth was collected, or by whom, and it cannot therefore be verified.

In our sample we also identified four bone fragments of sphenodontian origin. Sphenodontian remains are common in fissure infills, such as at Holwell, but have never before been recorded from the Westbury Formation. The only records of sphenodontian remains recovered from European marine sediments are from the Belgian Rhaetian, so far as

we are aware (Duffin 1996). Their presence in the marine sequence at Marston Road quarry is likely to be a consequence of proximity to land. Remains of the terrestrial fauna could easily have been washed out into the sea, especially very small and light bones. Due to their fragmentary and polished appearance, it cannot be ruled out that they may be reworked sediment, presumably from one of the nearby fissure infills, maybe even the fissures in the same quarry. Future sampling and comparison with these fissure fills is necessary to resolve this question.

Although the faunal assemblage in general is similar to those from other parts of the Westbury Formation, it matches the fauna of the Holwell quarry most closely, differing only in two of fifteen species (Duffin, 1980) - *Paleobates* and *Nemacanthus monilifer*, which are absent in our sample. *N. monilifer* and *Paleobates* are very uncommon in the Holwell fissures (Duffin, 1980), and their absence in the Marston Road samples might be due to small sample size. More convincingly however, is the presence of fossils that are not commonly found in the Westbury Formation; *P. raeticus*, *P. alpinum*, “*Colobodus*” and sphenodontians, which are all also found in the Holwell fissures (Kühne, 1947; Duffin, 1980; Fraser, 1994.). This makes the faunal composition of Marston Road remarkably similar to that of the fissure infills of Holwell, supporting earlier suggestions of Rhaetian age for these fissures (Kühne, 1947; Duffin, 1980).

5.2. Palaeoecology and palaeoenvironment of Marston Road

As mentioned above, the overall picture of the vertebrate fauna is similar to that found elsewhere in the Westbury Formation. This may be a true reflection of the fauna at Marston Road, or it could be a consequence of the mode of deposition of the sediment. If the bone beds are storm deposits, as has been suggested (Kent, 1968; MacQuaker, 1987, 1999; Allington-Jones et al., 2010), teeth from deeper parts of the basin could have been washed up on the shore and mixed with the sediment deposited *in situ*, creating the superficial impression of an homogeneous fauna. The short distance travelled by teeth and scales within the basin is unlikely to have resulted in any notable difference in abrasion compared to the non-transported teeth (Argast et al., 1987), making it difficult to distinguish between autochthonous remains and material transported for some distance.

For these reasons, a simple quantitative comparison may not tell us much about the Marston Road assemblage alone, but rather about Westbury bone bed assemblages generally. However, the Marston Road fauna is interesting because it contains taxa that are rare or absent elsewhere in the Westbury Formation, even though these fossils are low in numbers.

“*Colobodus*” is only reported from Holwell, Aust Cliff, and outcrops in Leicester (Duffin, 1999), *P. raeticus* is most common at Holwell, Aust Cliff and Garden Cliff, and *P. alpinum* has only been found at Holwell and Aust Cliff. Lepidosaur remains have, as far as we know, not been reported from anywhere else in the Westbury Formation.

Similarly to Marston Road, both Aust Cliff and Westbury Garden Cliff are interpreted as strand line, perhaps intertidal, deposits (Storrs, 1994). The bone bed at Aust Cliff contains a particularly rich invertebrate fauna (Duffin, 1978) – an environment ideal for placodonts, as discussed earlier. The ecology of *P. raeticus* is somewhat more enigmatic, since only fragmentary remains have been found. Storrs and Gower (1993) assigned it to Choristodera, a group of crocodile-like semi-aquatic diapsids, found in freshwater habitats. However, this is problematic because the skull contains the diagnostic features of choristoderes (Matsumoto and Evans, 2010), but only one cranial bone has been found of *P. raeticus*. Renesto (2005) suggested that *Pachystropheus* might be related to *Endennasaurus* from the Late Triassic of Italy, a possible thalattosaur, based on the common occurrence of 22 characters regarded by Storrs and Gower (1993) as unique to choristoderes. Whatever its correct phylogenetic placement, the similarities between *P. raeticus* and the slender, long-bodied choristoderes and thalattosaurs, indicate a similar, semi-aquatic, coastal lifestyle.

The shape of “*Colobodus*” teeth is very similar to those of durophagous species like *Paralepidotus*, indicating a similar, durophagous lifestyle. The reason why *Colobodus* seems to be restricted to shallower environments, and was not as widespread as other Rhaetian durophagous fish such as “*Lepidotes*” and *S. tomicus*, is very hard to identify because of the scarcity of material. However, the correlation of fauna and similar geology suggests *Colobodus*, *P. raeticus* and *P. alpinum* are indicative of a particular environment, namely shallow shoreline waters with a rich invertebrate fauna.

It could be argued that the absence of the above-discussed taxa from other sites simply is a consequence of insufficient sampling. Placodont teeth are quite rare, and have been confused with “*Lepidotes*” teeth previously (Duffin, 1980), and similarly, “*Colobodus*” is not common in the Westbury Formation. However, many of the Rhaetian bone bed sites and fissures have been studied and sampled for two centuries, and the complete absence of some species is unlikely to be a result of sparse sampling. Even so, quantitative studies are rare, and further research on fossil faunas, both vertebrate and invertebrate, of different parts of the Westbury Formation is necessary to get a fuller understanding of geographical and habitat variations.

5.3. Evidence for age of bedded and fissure deposits

The microvertebrate fauna described here is undoubtedly early Rhaetian, coming as it does from a thin representative of the Westbury Formation. The Rhaetian-Hettangian succession at Marston Road quarry was condensed to only 0.3–1 m in all, according to Richardson (1911), but evidence of the age of each successive thin bed, from bottom to top, has been provided by the vertebrate fossils in the basal, bone bed layer, and by marine invertebrates in the units above (Richardson, 1911; Copp, 1985).

The Holwell fissures, although only 300 m away, cannot be unequivocally linked in age without further investigation (Kühne, 1947). However, there are some independent indicators that some at least, and perhaps those that yielded the *Microlestes*/*Haramiya* from Cree's Quarry, might indeed also be Rhaetian. Wall and Jenkyns (2004) identify five fissure fill types in the eastern Mendips, ranging in age from Triassic to Middle Jurassic. The fissure fills are dated based on field relationships (do they cut, or are they cut by, dated units such as the marine bedded Rhaetian or Inferior Oolite?) as well as biostratigraphically informative fossils such as palynomorphs, foraminifera, ostracods, brachiopods, and ammonites, and strontium dating of belemnites. Importantly, the older fissures, generally filled with red mudstones and marls, were formed in tectonic fissures and solutional caves, and filled during the Late Triassic. Some, such as the Tytherington fissures, are early Rhaetian based on palynomorphs, with a mix of terrestrial and marine influences (Whiteside and Marshall, 2008). Stratigraphically younger are the Type 2.1 fissure fills, comprising grey, clastic limestones with excellent microvertebrate fossils, which are older than the Type 2.2 fills, as shown by cross cutting relations. The Type 2.2 fissure fills are dated as late Hettangian to early Sinemurian based on their marine invertebrate faunas (Wall and Jenkyns, 2004). The Type 2.1 fissures are then dated as Rhaetian to early Hettangian, with a preference for the Rhaetian based on the wealth of phosphatic material, and could perhaps correspond to the early Rhaetian Wedmore Stone Member of the Westbury Formation (Green and Welch, 1965), a shelly biosparite containing quartz fragments that yielded enigmatic large dinosaur bones called *Camelotia* and *Avalonia* (Galton, 1998).

These regional correlations are not conclusive. The close proximity of the *Microlestes*/*Haramiya* mammal teeth from fissures in Cree's Quarry, found by Moore (1867), and later reported by Simpson (1928), Kühne (1947), and Savage (1993), to the Marston Road bedded Rhaetian bone bed is suggestive, as is the earlier report by Plieninger (1847) of the same mammal teeth in the German Rhaetian bone bed, with associated fish teeth.

5.4. The last placodonts

The *Psephoderma alpinum* teeth from Marston Road represent some of the very last members of not only the species, but also of the entire order Placodontia. Placodonts were already in decline during the Late Triassic, with only two species surviving into the Rhaetian, both cyamodontoids. This is in stark contrast to the diverse placodont fauna of the Middle Triassic, with three cyamodontoid and three placodontoid genera, found in the eastern and western provinces of the Tethys (Rieppel, 2000; Li and Rieppel, 2002; Jiang et al, 2008; Zhao et al., 2008). Particularly diverse is the fauna of the Middle Triassic Muschelkalk in Germany, with six placodont species described (Rieppel, 2000). The Germanic epicontinental sea that these placodonts inhabited disappeared with the regression in the late Ladinian, and its placodonts with it (Pinna and Mazin, 1993a).

Late Triassic strata have so far not yielded any placodontoids, but cyamodontoids were still diverse in the Carnian, being present in the Alps and southeast China (Pinna and Mazin, 1993a; Li and Rieppel, 2002). The placodonts from Norian strata, however, are considerably less diverse, following a general trend of reduction in taxa of durophagous marine reptiles during this period (Kelley et al., 2014). The reason for their decline may have been habitat loss, as it coincides with a regression resulting in a shrinking of available shelf habitat. By the start of the Rhaetian, placodont diversity had diminished to only two species, *Psephoderma alpinum* and *Macroplacus raeticus* (Rieppel, 2000), and although the Rhaetian transgression initiated the spread of *P. alpinum* to the British Isles, extending its geographical range, the placodonts never regained their former diversity. *P. alpinum* has been described from Late Triassic strata in Italy (Pinna, 1975, 1976, 1978, 1979; Nosotti, 1987), Germany (Meyer, 1858; Ammon, 1878; Broili, 1920), Austria (Zapfe, 1976), Switzerland (Huene, 1911; Neenan and Scheyer, 2014) and Britain (Owen, 1858; Meyer, 1864; Moore, 1858; Osswald, 1930; Kühne, 1947), with the youngest specimens of mid-Rhaetian age (Pinna and Mazin, 1993a). Only one skull is known from *M. raeticus*, from the Kössen Formation of Germany (Schubert-Klempnauer, 1975). A summary of the palaeobiogeographic range of Late Triassic placodonts is given in Figure 12. Peyer (1931) described a placodont tooth from the Early Jurassic of Switzerland, but this was most likely from reworked Rhaetian strata (Wiedenmayer, 1963; Pinna, 1990). Placodonts hence seem to have gone extinct just before the end of the Triassic.

In Britain, the Cotham and Lilstock formations, which succeed the Westbury Formation, are interpreted as a time of regression (Hallam, 2004), and this may have contributed to the regional disappearance of placodonts. Derived cyamodontoids such as *P.*

alpinum developed an elongate, narrow and toothless rostrum, which bore ventral grooves leading to the internal nares, and which might indicate olfactory function (Rieppel, 2000; Li and Rieppel, 2002). It has been suggested that *P. alpinum* used its snout to search for endobenthic fauna in muddy sediments (Pinna and Mazin, 1993a). Powerful jaws and flat, crushing teeth allowed *P. alpinum* to break the shells of crustaceans, bivalves and gastropods, and the well developed body armour would have protected it from possible predators such as *Severnichthys acuminatus*, ichthyosaurs and plesiosaurs.

The feeding habits of *P. alpinum* would have constrained it to habitats with a rich benthic fauna of shelled invertebrates. Certain characteristics of the skull of *P. alpinum* suggest it might have fed on softer prey, such as crustaceans, rather than bivalves and brachiopods. Tooth replacement rates seem to have been slower in *P. alpinum* compared to other placodonts (Neenan et al., 2014), and the posterior part of the brain case is less robust than in other placodonts (Neenan and Scheyer, 2014). These morphological indicators for a softer diet are supported by the contemporaneous fauna present in the two formations in the Italian Alps that are particularly rich in placodont remains, the Rhaetian Calcare di Zu, and the Norian Calcare di Zorzini (Pinna and Mazin, 1993a). Both were deposited in a similar environmental setting, a carbonate platform, with shallow waters and a muddy, micritic seafloor (Lakew, 1990; Berra et al., 2010). In both cases, the fauna includes abundant crustaceans, although other invertebrates such as bivalves, echinoderms and brachiopods are also present (Lakew, 1990; Lombardo and Tintori, 2005; Berra et al., 2010). Periods of low oxygen partial pressures at the bottom related to fluctuations in sea level might have been responsible for the relatively scarce invertebrate fauna (Lombardo and Tintori, 2005). The environment imagined for the Calcare di Zu and Calcare di Zorzini is quite different from the deeper-water Westbury Formation, dominated by black shales. Even though the Westbury Formation contains numerous bivalve fossils, these are mostly limited to concentrated “shell-beds”, which may have formed by winnowing of material (MacQuaker, 1999). It is therefore unsurprising that placodonts are not common in the Westbury Formation, and that the only sites where they have been found are in shoreline deposits of limestone and sandstones, where the black shales are much less prominent. The presence of placodonts at the Marston Road quarry is thus an indication that the waters around the Mendip Hills archipelago were quite different from the rest of the basin, and more similar to the shoreline environments imagined for Calcare di Zu and Calcare di Zorzini.

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Fig. 1. Map of the Marston Road locality, with the Marston Road Quarry marked with a red star. © Crown Copyright and Database Right 2015. Ordnance Survey (Digimap Licence).

Fig. 2. Excavation at Marston Road Quarry, carried out by the Nature Conservancy Council (now English Nature) in July, 1985, when the A361 was straightened, and the old quarry obliterated. (A) View along the old A361, looking west towards Holwell Quarry, in the background, and the Marston Road site on the right. (B) Excavated site, showing the margin of the realigned road, the gently folded Carboniferous Limestone to the left, and front. On top of the Carboniferous Limestone, towards the right, sits the succession of Rhaetian (dark grey mudstone) and Inferior Oolite (grey, nodular limestone). Photographs © Natural England / Mike Harley.

Fig. 3. Palaeogeographic reconstruction of the Bristol area during the Late Triassic (from Whiteside and Marshall, 2008). Grey areas represent palaeo-highs.

Fig. 4. Drawing of the Marston Road Quarry by Moore, produced around 1850.

Fig. 5. Moore's annotated photograph of the Marston Road Quarry, produced around 1850. The label at top left is the stratigraphic key to the numbered nits in the photograph.

Fig. 6. Section of the Marston Road Quarry, showing Rhaetian sediments lying between Carboniferous Limestone and Inferior Oolite. Photograph taken by Mike Curtis in 1984.

Fig. 7. The Marston Road Quarry, photograph taken by Mike Curtis in 1985. (A) Overview, and (B) Interpretation of geology, based on Curtis' field sketches and Copp's (1985) description.

Fig. 8. Chondrichthyan teeth. (A–D) *Lissodus minimus* anterior tooth (BRSUG 29371-1-1776), labial (A) and occlusal view. (B), posterior tooth (Cf 16859), lingual (C) and occlusal view. (D). (E–F) *Hybodus cloacinus* anterior tooth (Cf 16859) lingual (E) and labial view. (F). (G–I) *Synechodus rhaetianus* anterolateral tooth (BRSUG 29371-1-1604:1), lingual (G) and labial views, (H), posterior tooth (BRSUG 29371-1-1604:2) lateral view (I). (J–K) *Rhomphaiodon minor* anterior tooth (BRSUG 29371-1-1513), lingual (J) and labial views (K). (L–N) *Duffinselache holwellensis* lateral tooth (BRSUG 29371-1-1590:2), lingual (L),

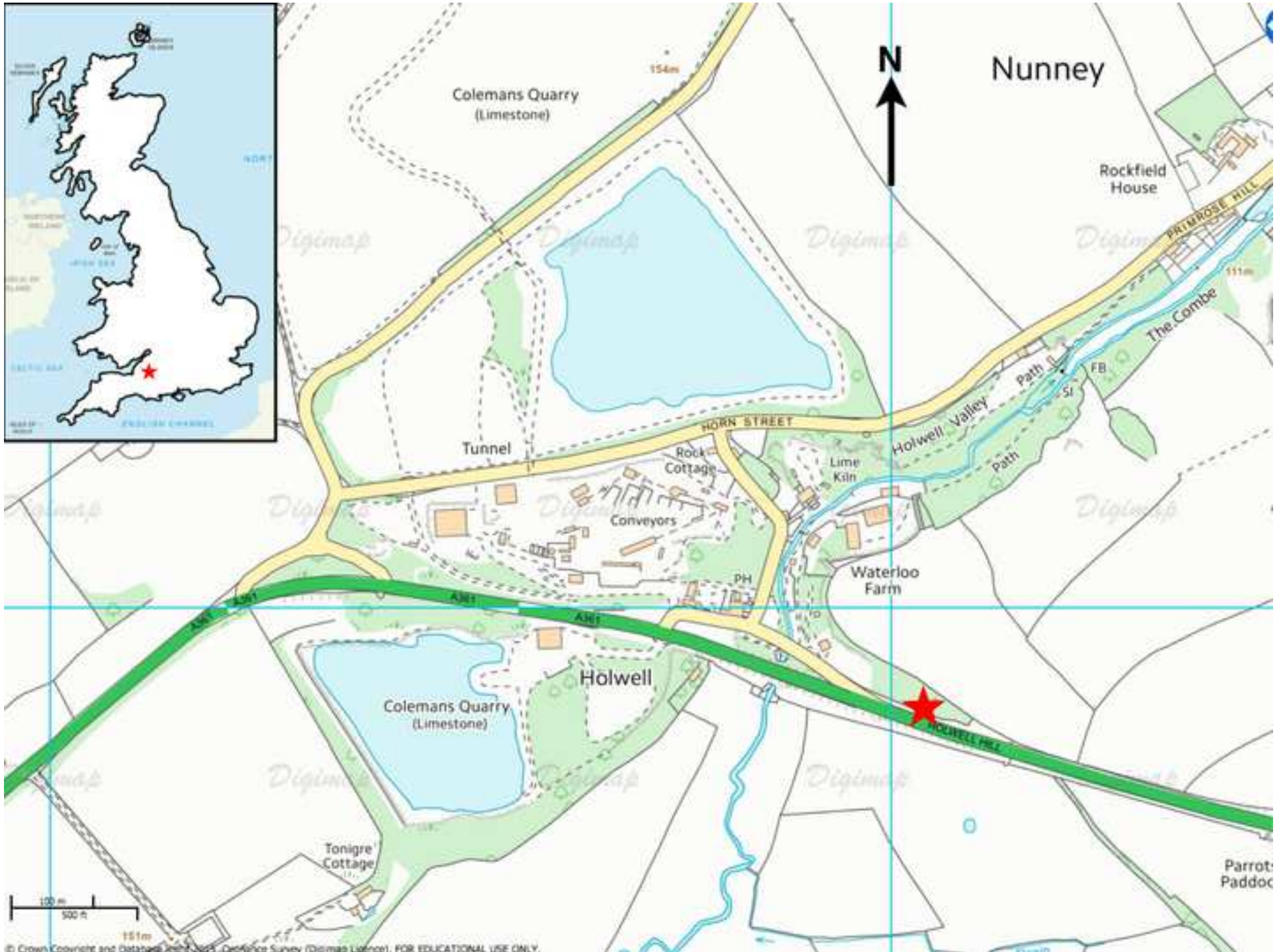
labial (M) and occlusal views (N). (O–P) *Pseudocetorhinus pickfordi* tooth (BRSUG 29371-1-1589) lingual (O) and labial views (P). (Q) *Pseudodalatias barnstonensis* tooth (Cc 5902), lateral view. All scale bars equal 1 mm.

Fig. 9. Actinopterygian teeth. (A) *Gyrolepis albertii* tooth (Cf 16718). (B–F) *Severnichthys acuminatus* teeth; (B–E) *Saurichthys longidens*-type, B (Cf 16686:1), C (Cf 16688:1), D (Cf 16686:2), E (Cc 5898), (F) *Birgeria acuminatus*-type (Cf 16892). (G–H) *Sargodon tomicus* incisiform tooth (BRSUG 29371-1-407), lateral view (G), molariform tooth (BRSUG 29371-1-1568:1) lateral view (H). (I) “*Lepidotes*” tooth (BRSUG 29371-1-1554), lateral view. (J) “*Colobodus*” tooth (BRSUG 29371-1-1561), lateral view. (K–P) Jaw fragments; (K–L) BRSUG 29371-1- 92/1, in occlusal (K) and lateral (L) views, (M–N) BRSUG 29371-1-92/2, in occlusal (M) and lateral views (N), (O) BRSUG 29371-1-92/3, in occlusal view, (P) BRSUG 29371-1- 92/4, in lateral view. All scale bars equal 1 mm.

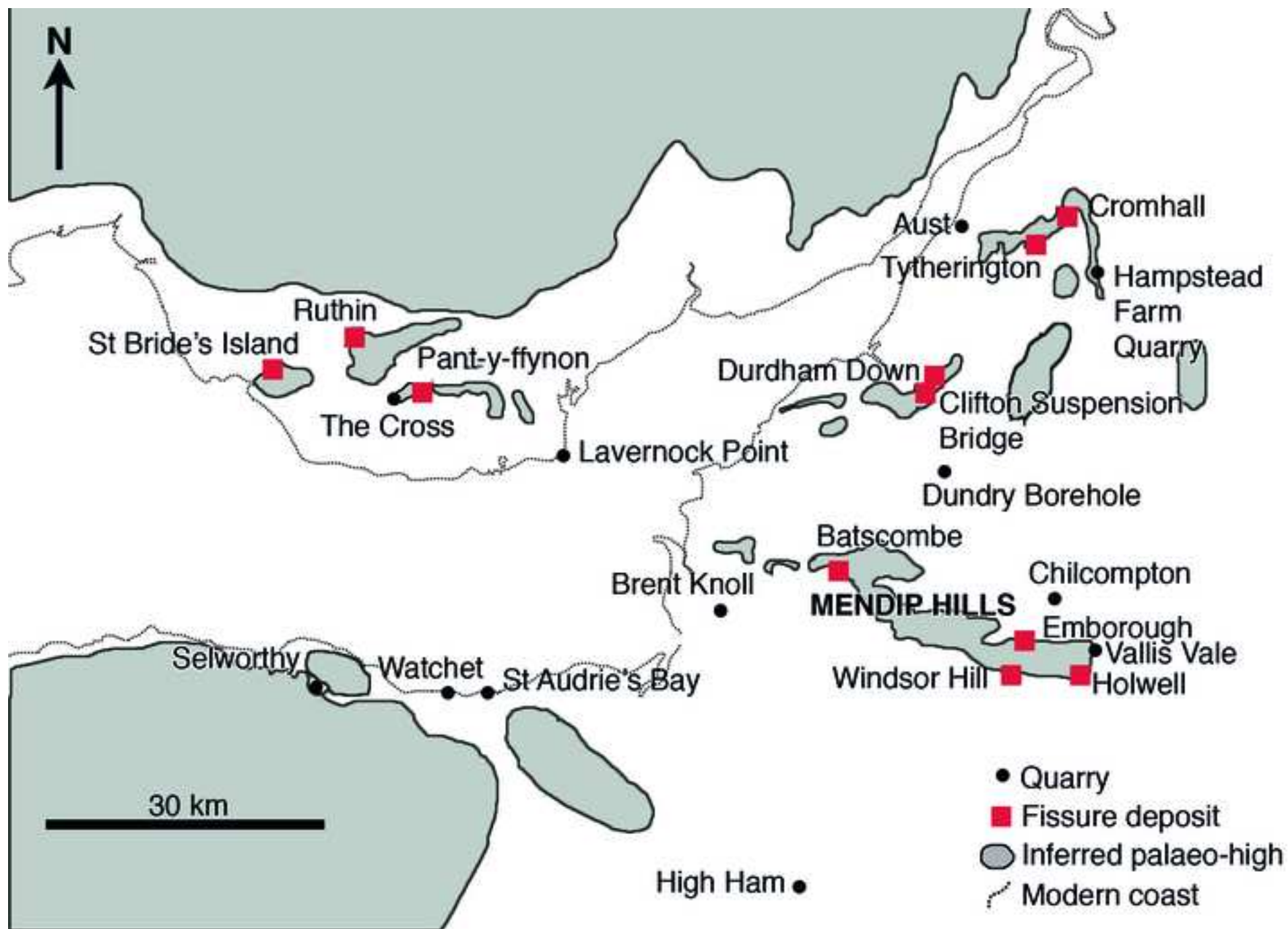
Fig. 10. Reptilian remains. (A–D) *Pachystropheus raeticus* vertebra (BRSUG 29371-1-826:3) in right lateral (A), left lateral (B), posterior (C) and anterior (D) views. (E–F) *Psephoderma alpinum* posterior maxillary tooth, in occlusal (E) and lateral (F) views. (G–H) *Pachystropheus raeticus*, centrum of vertebra (BRSUG 29371-1- 826:1) in articular (G) and lateral (H) views. (I–N) Lepidosaurian bone fragments; (I–J) metatarsal (BRSUG 29371-1-882/1) in dorsal (I) and ventral (J) views, (K–L) metatarsal (BRSUG 29371-1-882/2) in ventral (K) and dorsal (L) views, (M) bone fragment (BRSUG 29371-1-882/3), (N) bone fragment (BRSUG 29371-1-882/4). All scale bars equal 2.5 mm.

Fig. 11. A: Relative proportions of all material. Total number of specimens: 4497. The category “Other” includes coprolites, prismatic cartilage, osteichthyan jaw fragments, osteichthyan ring centra, *P. raeticus* vertebrae and fin spines. B: Relative proportions of chondrichthyan and osteichthyan teeth, excluding fragmentary teeth (as defined in “Methods”). Total number of specimens: 1072. The category “Other” includes *Pseudocetorhinus pickfordi* and *Hybodus cloacinus*.

Fig. 12. Palaeobiogeographical range of placodonts in the Late Triassic (Norian-Rhaetian). Black dots represent localities where placodonts have been found (referenced in text), shaded grey areas indicates inferred palaeo-highs (after Ziegler 1990).









Marston Road Section

East eastern Carboniferous
Limestone

1. *Lepidodendron*
2. *Lepidodendron* with
many specimens
3. Thin band of black
limestone
4. *Lepidodendron* limestone
5. Band of massive sand
probably *Lepidodendron*





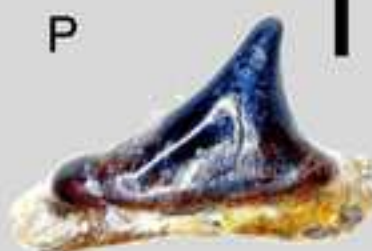


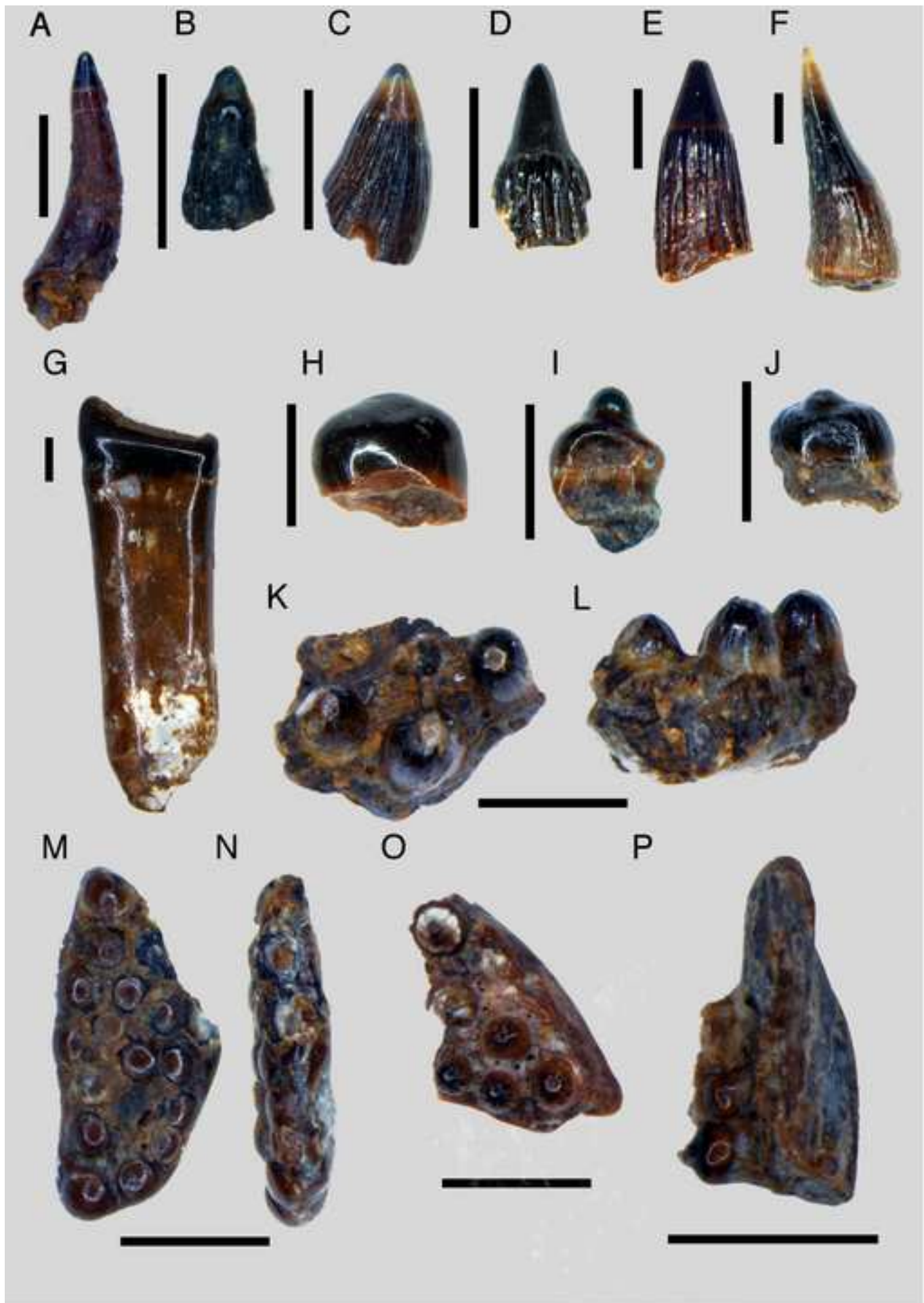
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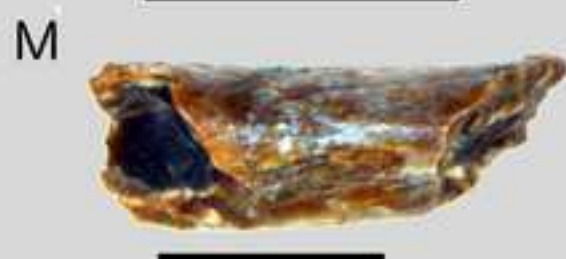


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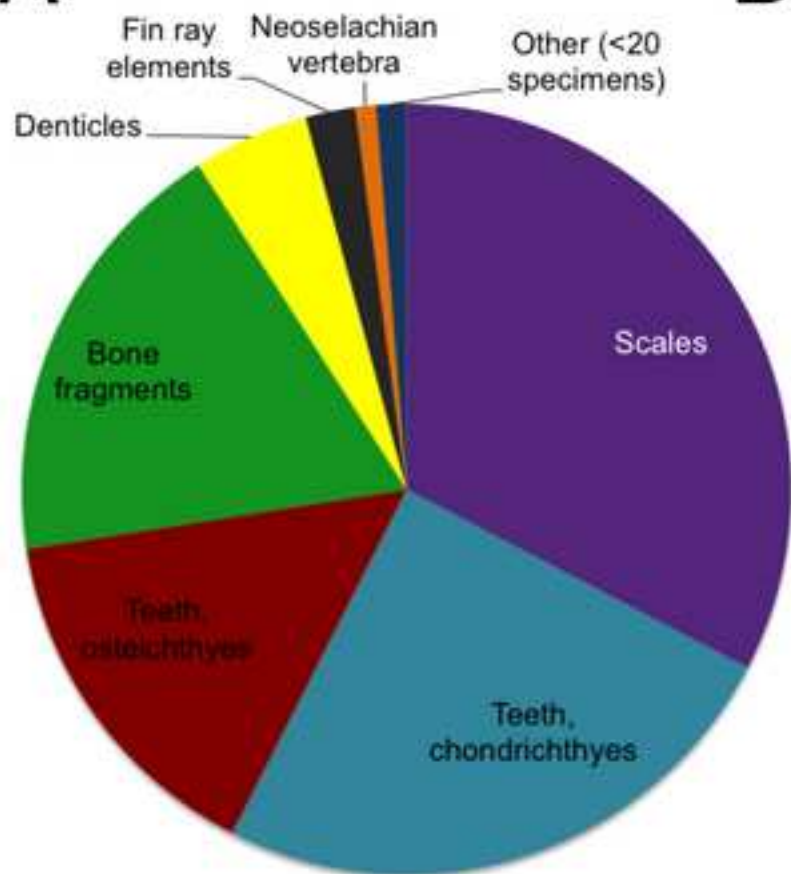








A



B

